

OCCURRENCE OF THE INSECTIVORE GENUS
MICROPTERNODUS IN THE JOHN DAY FORMATION
OF CENTRAL OREGON

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INTRODUCTION

A rostrum and part of a left mandible of a small insectivore, still held in occlusal position by the matrix, was found in an exposure of the John Day formation during the summer of 1956 by Anthony Morgan of Monument, Oregon. The boy's father, Milton Morgan, who had collected fossils in the valleys of the John Day River for a number of years, immediately recognized the specimen as different from the others he had seen. He presented the specimen to the Museum of Paleontology with the request that it be described by the senior author.

The junior author has undertaken a study of the vertebrate sequence in the John Day beds. This research is being done in conjunction with the stratigraphic studies of the formation by Richard V. Fisher of Santa Barbara and Richard L. Hay of Berkeley, both at the University of California. It will be some time before these studies are completed; consequently, because of Mr. Morgan's request, the description of the insectivore is presented at this time.

The first information on the genus *Micropternodus*, to which the John Day specimen belongs, appeared when W. D. Matthew (1903) described *M. borealis* from a mandible which was found near Pipestone Springs, Montana. Then in 1954, T. E. White published on *Kentrogomphios strophensis*, based upon the anterior part of a cranium and a referred right mandibular fragment which were found about one mile north of Canyon Ferry, Montana. Two other man-

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dibular fragments from Pipestone Springs were referred to *Micropternodus* by Jean Hough (1956). One of these (Fig. 17) was subsequently identified as *Geolabis* by McKenna (1960). McKenna also observed that Hough's Fig. 16 is not referable to the same genus as Fig. 17, but did not confirm its reference to *Micropternodus*. Additional specimens, including the rostrum of a cranium and ten mandibular fragments found at Pipestone Springs by J. LeRoy Kay, were studied by Dale A. Russell (1960). Russell concluded that *K. strophensis* White was a synonym of *M. borealis* Matthew. He reviewed all of the publications and statements about the genus as well as the discussions and opinions on its broader relationships in the order Insectivora. Reed (1956) has suggested that the humeri from Pipestone Springs, which he described (1954) as *Cryptoryctes kayi*, may belong to *Kentrogomphios* (= *Micropternodus*). Unfortunately no limb bones have been found in association with any specimen to support this plausible conclusion.

The only other genus clearly referable to the Micropternodidae is *Clinopternodus* Clark, 1937, from an upper member of the Chadron formation in South Dakota.

The association of the upper and lower teeth in the John Day *Micropternodus* confirms the reference of these teeth in the types and referred specimens from Pipestone Springs and Canyon Ferry. It also extends the vertical range of the genus from early Oligocene (Chadronian) to the early Miocene (Arikareean).

ACKNOWLEDGEMENTS

We wish to commend Mr. Milton Morgan for his appreciation of the true value of the specimen found by his son. He not only recognized the fossil as representing a mammal not previously discovered in the John Day formation, but felt that its importance could be fully realized only if it were described by a professional paleontologist. This attitude by amateur paleontologists and "rock hounds" is becoming progressively more important as thousands of these people swarm over the countryside in search of fossils and rocks to satisfy their curiosity.

We are grateful to Dr. Craig Black of the Carnegie Museum for the loan of the type of *Micropternodus borealis*, and to Dr. C. L. Gazin of the U. S. National Museum for permission to study the type of *Micropternodus strophensis*. The illustrations were done by Owen J. Poe. All measurements are in millimeters.

ABBREVIATIONS

AMNH	American Museum of Natural History
CM	Carnegie Museum
UCMP	University of California Museum of Paleontology
USNM	United States National Museum

Order—INSECTIVORA

Superfamily—ERINACEOIDEA

Family—MICROPTERNODIDAE

Family Diagnosis.—About the size of moles; probably fossorial (see Reed, 1954; 1956). Rostrum long, moderately wide and deep (*Micropternodus borealis*), or short, wide and deep (*M. strophensis* and *M. morgani* sp. new.); sutures tend to fuse early; infraorbital foramen short and large; no lacrimal tubercle.

Upper cheek teeth hypsobranchiodont; ectolophs slant strongly lingually; three upper incisors, I¹ greatly enlarged in *M. borealis*, not known in other species. Canines with one root. P¹ not present. Diminutive alveolus for P² in *M. borealis* and *M. strophensis*, one root; P² not present in *M. morgani*. P³ nearly triangular; main cusp an oblique sectorial blade with steeply inclined posterior edge; no anterior basal cusp; protocone extremely reduced. P⁴ submolariform; small hooklike cusp behind and above metastyle at posterior end of sectorial blade of ectoloph; paracone high, somewhat trenchant, anterior in position; protocone almost directly linguad of paracone, sharp triangular outline, half as high as paracone; inner part of tooth wide; hypocone separated from protocone by V-shaped emargination of lingual border of tooth; talonid shelf as in molars, wide, with shallow basin between hypocone and ectoloph, labial end separated from metastyle by deep anterior emargination.

M¹ and M² with slight labial basal cingula; parastyles and metastyles at ends of long thin winglike crests from paracones and metacones, with thin hooklike cusps anterior to parastyles and posterior to metastyles, especially on M²; ridge on labial surface anterolabial of metacone usually present (near position of mesostyle of some mammals), but fades out before it reaches basal cingulum, evidently originates from metacone not from cingulum; wide emargination of ectoloph between stylar cusps; paracones and metacones distinct but not widely separated; protocones with relatively narrow V-shaped angles formed by protolophs and metalophs; talon wide anteroposteriorly and even more extended transversely than in P⁴,

but with emargination of posterior outline between labial ends of talons and metastyles; no anterior basal cingula.

Lower cheek teeth hypsobrachiodont. Alveolus for I_2 larger than those for I_1 and I_3 . Canine alveolus apparently for one root. P_3 much larger than P_2 , somewhat submolariform. P_4 and lower molars with very high and anteroposteriorly narrow trigonids, with upper half of crowns curving posteriorly; talonids equal to or narrower than trigonids and about half as high or higher; anterior spur of hypoconid connecting on posterior surface of protolophid at midline of tooth on lower molars.

Generic diagnosis:

Micropternodus: smaller than *Clinopternodus*; lower canine, crowns of P_3 , P_4 , M_1 not as procumbent nor lingually curved, tips of crowns more recumbent than in *Clinopternodus*; P_2 present although small; P_3 higher crowned than in *Clinopternodus*; M_1 talonid almost equal to height of trigonid.

Clinopternodus: larger; lower canine, crowns of P_3 , P_4 , M_1 , quite procumbent, lingually curved; tips of crowns not recumbent; P_2 absent; P_3 lower crowned than in *Micropternodus*; M_1 talonid equal to two-thirds height of trigonid.

***Micropternodus morgani* NEW SPECIES**

Figures 1 and 2

Holotype.—Rostrum with premaxillae broken off back of I^1 , palate and most of dorsal part of rostrum preserved; right and left I^2 broken off; right I^3 broken off, left I^3 preserved; tips of canines broken off; no alveoli for first or second premolars; P^3 and P^4 present on both sides; all molars present except left M^3 ; posterior part of cranium missing as far as anterior ends of orbits. Part of right mandible with P_3 to M_3 in place. UCMP 60801.

Type Locality.—Surface of white tuffaceous claystone, about 130 feet below welded tuff, a few feet below brownish nodular tuff; NW $\frac{1}{4}$ SE $\frac{1}{4}$, Sec. 14, T. 10 S., R. 27 E., Courtrock quadrangle, Grant County, Oregon, Univ. Calif. Loc. V5950.

Formation.—Middle beds of John Day.

Age.—Earliest Arikareean; early Miocene.

Specific Diagnosis.—Proportions and shape of cranium much more like that in *M. strophensis* than *M. borealis*; deeper than in either of those species; rostrum wider than in *M. strophensis*, much more so than in *M. borealis*; forehead more steeply inclined; depressions on

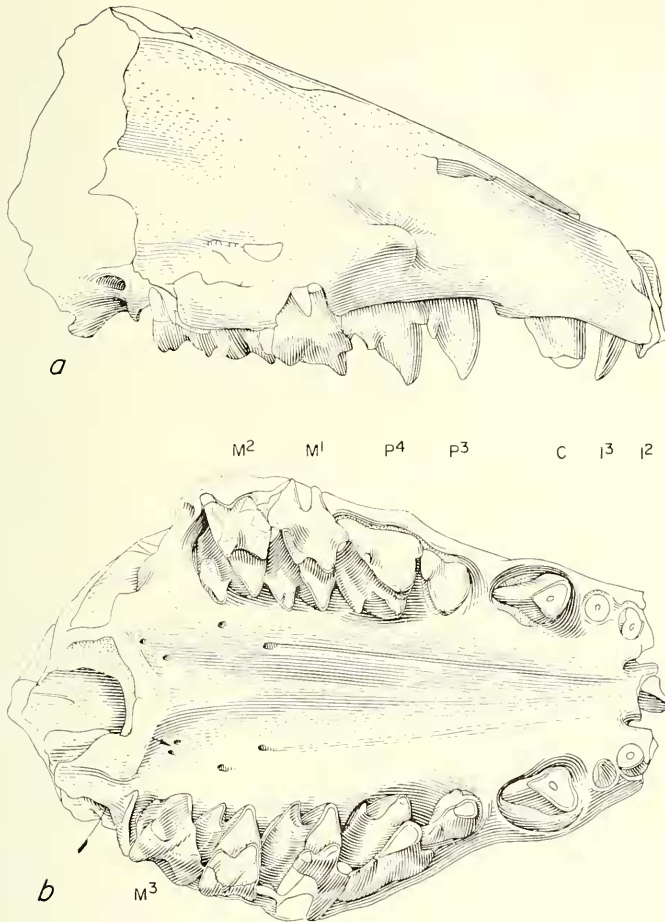


Figure 1. *Micropternodus morgani*, n. sp., UCMP 60801, middle John Day fm., Oregon. *a*, rostrum, right lateral view; *b*, rostrum, palatal view.

maxilla in front and behind canine even shallower than in *M. strophensis*.

Upper canine twice as large as in Oligocene species. Cheek teeth higher crowned, crowns and even roots with more procumbent orientation than in other species. No indication of tiny alveolus for P^2 . P^3 larger, higher crowned, main cusp with greater posterior curvature than in *M. strophensis*, and with tiny labial cusp posterior to metastyle at end of sectorial blade; partly overlapped by P^4 ; greater tendency to develop posterolingual shelf on P^3 than in *M. strophensis*; other teeth not significantly increased in size.

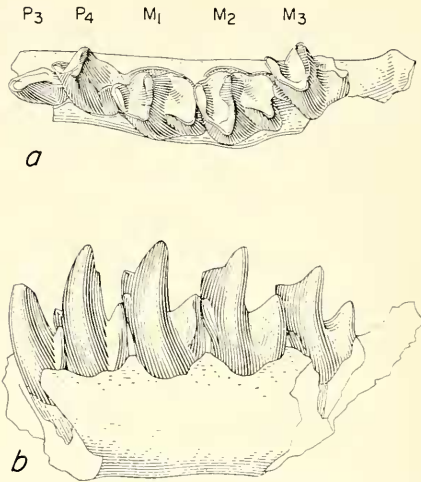


Figure 2. *Micropternodus morgani*, n. sp., UCMP 60801, middle John Day fm., Oregon. *a*, left mandible, occlusal view; *b*, same, left lateral view.

Paracone on P^4 not demarcated from paraconal blade; parastyle anterolabial to sectorial blade; protocone markedly procumbent; hypoconal shelf with conspicuous labial expansion and with less abrupt descent to protocone and sectorial blade than in *M. strophensis*; parastyle not as prominent as in Oligocene species.

Slight indication of anterior bulge on protoloph at anterolingual base of paracone in upper molars, absent on M^1 ; only faint trace of protoloph at anterolabial base of paracone connecting through to parastyle; parastyle, paracone and protocone less distinct from intervening parts of protoloph than in other species; paracone and metacone closer together than in the other species, and parastyle and metastyle less pronounced than in Oligocene species; anterior (protoloph) and posterior (metaloph) wings of protocone close narrow basin between paracone, metacone and protocone; protocone more procumbent than in *M. borealis* or *M. strophensis*; no "mesostyle" on M^1 , slightly developed on M^2 ; labial cingulum flattened; small posterior crest of hypoconal shelf connected to hypocone; hypoconal shelf with greater labial expansion than in Oligocene species, and more restricted emargination of posterobasal outline.

M^3 longer than in *M. strophensis*; protoloph at anterior edge of tooth; protocone and paracone not crescentic; protocone, paracone and parastyle of almost equal height and not as distinct on protoloph as in *M. strophensis*; crest from paracone to anterolabial end of

tooth not as elongate and parastyle not as bulbous as in *M. strophensis*; small talon with tiny hypocone.

Mandible more robust than in Oligocene species and with M_1 and M_2 larger; P_3 less molariform and smaller than in *M. borealis*; less suggestion of trigonid pattern; markedly curved posteriorly, nearly oval in outline except at base; talonid more reduced than in *M. borealis*, with single cusp on posterolabial corner and labiad of paraconid of P_4 ; paraconid and hypoconid of about equal height: paraconid of *M. borealis* is much higher; anterior cingulum as nubbinlike process; strong posterior curvature; talonid more transversely reduced than in *M. borealis*, with single cusp on posterolabial corner; hypoconid extends backward with tip resting under paraconid of M_1 ; no shelflike union of labial base of talonid with trigonid as in *M. borealis*; no diastema between P_4 and M_1 .

Lower molars high crowned, somewhat procumbent in lower half of crown, and curved posteriorly in upper third; paraconids not as high in relation to heights of metaconids and not located as far lingually as in *M. strophensis*; trenches (metaflexids) between paraconids and metaconids longer transversely and deeper than in *M. strophensis* or *M. borealis*; nubbinlike process replaces anterior cingulum; hypoconids much higher and more distinct than in *M. strophensis*; hypoconulids thin and transversely elongate; entoconids do not stand out as distinct cusps on hypolophids; talonids wider than in *M. strophensis*; no labial shelflike connection from base of hypoconid to base of protoconid.

DESCRIPTION

CRANIUM:—The rostrum, palate, most of the frontal, and part of the orbital areas of the cranium are preserved. In some respects it is more completely preserved than the Canyon Ferry specimen but in others it is not. Although the John Day specimen represents a young animal the sutures are fused beyond recognition. Most of the area of the nasals is broken away as far back as the end of the canine root. This exposes the turbinals. Much of the anterodorsal surface of the cranium is preserved. The part remaining reaches a point 4.5 back of M^3 . This is probably opposite the anterior end of the orbit.

Only the medial wall and floor of the infraorbital canal are preserved. Its transverse diameter appears to have been 1.4. Both sides of the rostrum are in excellent condition. The palate is nearly perfect as far forward as the posterior parts of the incisive foramina. The anterior extremities of the premaxillaries are broken off, con-

sequently their anterior extension and shape cannot be determined. They evidently are broken off back of the alveolar border of I^1 , therefore there is no evidence of the size or position of that tooth. The tooth rows are represented from I^2 - M^3 on the left side, and I^2 - M^2 on the right. Both P^1 and P^2 were never present in the John Day specimen.

The rostrum is 7.9 wide behind the canine and 4.4 deep above the alveolus of P^1 . It also appears to have been relatively short. This is partly reflected in the absence of P^2 and in the absence of a diastem between the canine and P^3 . The anterior part of the rostrum seems to be longer in *M. borealis*, although the length of the molar series is about the same in both species. On the lateral surface the bone is not bulbously expanded over the root of the canine, although the canine root extends posteriorly to a position above the anterior end of P^1 . There are only slight, nearly vertical expansions of the bone above P^3 , but a prominent one occurs above P^4 . The swelling above P^4 forms the anterior end of a diminishing ridge which covers the shorter labial roots of the molars and forms the floor of the infraorbital canal. There is also a sulcus above the labial root of P^4 . Its depth is accentuated by the ridge. Another sulcus occurs above the infraorbital canal. Three longitudinally aligned nutritive foramina are present just medially of each canine root on the dorsal part of the rostrum. Another foramen is ventral to the left P^3 root protuberance, but is absent on the right side. There are no foramina above or between the roots of P^4 and M^1 .

The palatine grooves are long and distinct. They extend from the anterior palatine foramina to the incisive foramina. These grooves form the lateral margins of an elongate median surface that is more depressed than the areas on both sides of the palate. A low but sharp crest is present along the midline. The anterior palatine foramina lie opposite the posterior border of M^1 . There are four smaller foramina near the posterior end of the palate. Of these, two (the left, not visible in Fig. 1b, is indicated by the short arrow) lie just in front of, and pierce, the palatal torus. A large postpalatine foramen (fig. 1b, long arrow) is back of M^3 . *M. strophensis* clearly displays all these foramina. However, an additional pair a short distance anterior to the palatal torus were not observed in the Canyon Ferry specimen.

Upper teeth:—The dental formula differs from that in *M. borealis* and *M. strophensis* in the absence of any indication of P^2 . This reduction is not surprising in *M. morgani*, because the alveoli in the

Oligocene specimens are already conspicuously reduced. All of the other upper teeth are represented in *M. morgani* except the right M^3 and the front incisors, which were lost when the supporting bones were eroded away.

Crowns of both of the second upper incisors, I^2 , were destroyed, but the root with most of the basal enamel surface is preserved. The transverse diameter is 0.7. It is rather widely oval in cross-section and was probably a caniniform tooth. The root extends 2.3 upward and backward where it appears to terminate near and possibly above the end of the root of I^3 . The crown evidently was less vertical than in I^3 . A very short diastem (.4) separates I^2 and I^3 on the right side, but on the left side the teeth are in contact.

I^3 is caniniform, also oval in cross-section and with a transverse diameter of 0.9. Its crown is vertical. A carina on the posterolabial side forms the edge of a worn surface. The tooth is apparently larger than in *M. borealis* as determined from the relative sizes of the alveoli. A pit for the reception of the lower canine is present between the alveolus of I^3 and the canine, as in *M. borealis*. The anterior end of the pit in *M. morgani* is so close to the alveolus of the canine, however, that the rim between the pit and the alveolus is almost nonexistent.

The tips of both canines are missing but the basal cross-sections are triangular in outline. The long axis of the triangle is anteroposterior. In the basal half of the crown the anterior surface is slightly concave but the right canine shows the anterior border becoming convex toward the tip. The enamel is thickest on the anterior surface of the canines and diminishes to almost nothing at the posterior edge. Although the alveolus is larger than that of *M. borealis*, the two are similar in outline. The canine does not completely fill the alveolus, evidently because it is a young specimen. The parts preserved indicate a length of crown much less than that visualized by White (1954, fig. 43) for *M. strophensis*. Nevertheless, it extended below the level of the apices of P^3 and P^4 .

P^2 has been lost. The rostrum has been so foreshortened that the diastema between C and P^3 is only a thin lamina of bone not more than 0.2 in thickness. If the canine were fully erupted the diastema would not be apparent.

P^3 is nearly triangular. The paracone is extremely high and curved posteriorly at its apex. A long, steeply inclined, posterior, sectorial blade is less oblique in orientation than in *M. strophensis* and the labial surface is more concave anteroposteriorly. This con-

cavity is emphasized by a prominent labial paraconal ridge and by the distinctness of the short metastyle near the upper posterior corner. The metastyle emerges on the labial side of the posterior paraconal blade just anterior to a tiny stylar cusp on the extreme posterolabial corner of the tooth. A talon is not apparent. The small protocone appears to be closer to the anterior end of the tooth than in *M. strophensis*. The anterior basal outline of the tooth is convex transversely, and there is no anterolabial basal cusp. The height of the paracone is 2.5, whereas the metastyle is 1.2. The roots cannot be seen, but there are probably three as in *M. borealis*. On the whole P^3 is little more molariform than in the Oligocene species.

P^4 is submolariform and, of course, larger than P^3 . It is more molariform than in *M. strophensis* and much more so than in *M. borealis*, especially in the orientation of the sectorial blade. The sectorial blade is less oblique than in *M. strophensis*, which is less so than in *M. borealis*. Furthermore the labial surface appears to be less concave anteroposteriorly than in either of the Oligocene species. The concavity, however, appears to be relatively wider in *M. morgani* than in *M. strophensis*. In *M. borealis* the concavity is narrower and deeper than in *M. strophensis*. *M. morgani* differs from both of the other species in the presence of an extremely flattened cingulum-like structure that extends backward and upward from the parastyle to the metastyle. A small stylar cusp (metastylule of White [1954]), occurs on the posterolabial corner as in *M. borealis*, but it is more widely separated from the metastyle than in that species. The small posterior stylar cusp is overlapped by the parastyle of M^1 . The small stylar cusp is the "hooklike" cusp referred to by Russell (1960); it is, however, not hooklike in *M. morgani*, and is more reduced than in *M. borealis*. The paracone (parametacone of White, 1954) is approximately twice as high as the protocone, and the protocone about twice as high as the hypocone. The talon is wide, slants dorsolabially, and is basined between the hypocone and paracone. The protocone is broader anteroposteriorly and labially flatter than in *M. borealis*. There is no cingulum posterior to the hypocone as in *M. borealis*. The talon in *M. morgani* is much wider transversely than in *M. borealis* and *M. strophensis*, consequently the emargination of the posterior basal outline between the outer end of the talon and the metastylar area is greatly reduced in *M. morgani*. The depressed talon shelf slopes upward to the emargination. The depression is overshadowed by the anterolabial corner of the tooth behind and does not show in the illustration. The height of crown of the tooth

as measured from the bifurcation of the roots is 3.7, whereas it is estimated to have been 2.2 in *M. borealis*.

M¹ and M² are grossly alike but differ in certain details. M¹ is slightly larger, has no labial ridge ("mesostyle") slightly anterolabial to the metacone on the upper part of the crown as in M². The "mesostylar" ridge tends to fade out toward the base of the crown on M². This ridge has been called a "mesostyle" but its homology with that structure is doubtful because it does not connect to a basal cingulum and there is no mesostyle in the early erinaceoids from which this genus probably evolved.

On M¹ and M² the protoloph passes to the anterolingual base of the paracone where it forms a slight indication of an anterior bulge on M² which is absent on M¹. From that point there is only a faint trace of the protoloph connecting across the paracone to the parastyle. In *M. borealis* the protoloph forms a prominent bulge on M¹ and a less conspicuous one on M², and in both teeth the connection to the parastyle is incomplete. This is one of the characters that *M. borealis* shares with *M. morgani*. The protoloph of *M. strophensis* has slightly formed bulges on both M¹ and M²; but whereas on M¹ it passes along the anterior surface of the tooth to the parastyle, on M² the connection is incomplete. The protolophs are higher than the metalophs. Protoconules and metaconules are not apparent. The parastyles on M¹ are somewhat less prominent in *M. morgani* than in *M. strophensis*, and much less so than in *M. borealis*. The M² parastyles and metastyles of *M. morgani* are destroyed. The parastyle, paracone and protocone are less distinct from the intervening parts of the protoloph than in the other species. The paracone and metacone are highest in M¹, and become progressively more widely separated from M¹ to M³. Nevertheless the proximity of the paracones and the metacones are conspicuous features in *Micropternodus*. They are closer together in *M. morgani* than in the other species. The anterior (protoloph) and the posterior (metaloph) wings of the protocone close the narrow basin between the paracone, metacone and protocone. In this respect *M. strophensis* more closely approaches *M. morgani* than *M. borealis*. The sectorial ectolophs slant inward, and with wear the thickened enamel on the lingual sides of the paracones, metacones, and protocones accentuates this attitude. The metastyles on M¹ are less pronounced in both *M. morgani* and *M. strophensis* than in *M. borealis*. The labial cingulum is flattened in the upper third of the distance between the bases and the notch between the paracone and metacone. The pro-

tocones are nearly as high as the paracones and metacones. The hypocone is prominent and is separated from the protocone lingually by a deep vertical cleft. Farther labially, however, the hypoconal crest connects to the base of the metaloph. There is no small crest at the posterior edge of hypoconal shelf as in Oligocene species. The dorsolateral hypoconal shelf has a greater labial expansion than in Oligocene species. As in P^1 the posterior basal outlines of the molars have a reduced emargination between the labial ends of the talons and the metastylar areas.

M^3 has an elongate, rather narrow, triangular outline. The protoloph lies at the anterior edge of the tooth, whereas in *M. strophensis* the loph is located well back of the anterior edge. The protoloph is a straight, obliquely transverse blade. The contained protocone, paracone, and parastyle are of almost equal height and much less distinct from intervening parts of the protoloph than in *M. strophensis*. The parastyle is sharply crested and not as prominently extended anterolabially, nor as bulbous as in *M. strophensis*. Beyond the parastyle on the anterolabial corner of the tooth is a small hooklike cusp (parastylule of White, 1954), but this little cusp is only slightly developed. On the labial surface the parastyle is separated from the "mesostyle" by a deep vertical depression. The "mesostyle" is larger than on M^2 , forms the middle angle of the W-pattern, and appears to have been derived from the anterolabial corner of the metacone. The metacone is partly broken off; the metaloph is absent, leaving a rather wide vault opening posterolingually between the protoloph and the metacone. The metastyle is absent and leaves the W-pattern incomplete on M^3 . A small talon and hypocone are present, whereas in *M. strophensis* the talon is even smaller and there is no hypocone.

MANDIBLE:— Only the part of the left mandible with P_3 to M_3 is preserved but the horizontal ramus is uniform in depth (3.4) at least between P_4 and M_3 . It is more robust than in *M. borealis* and *M. strophensis*.

There has been some uncertainty about the presence of the first two lower premolars of *M. borealis*. This area is not preserved in our specimen but it is important in the generic diagnosis. In his original description Matthew (1903) states: "Molars and especially premolars are short, high, and recurved; P_4 submolariform, with small anterior and internal trigonid cusps and strong basal heel. P_3 much smaller and simpler, with small heel and no accessory cusps. P_2 is small and one rooted. . . . No diastemata except a slight one behind

P₂." In 1909, p. 543, in reference to the type, he states, however, that there are four premolars. Evidently sometime after his first paper appeared the specimen was carefully prepared revealing a tiny alveolus in the diastema mentioned above. This is clearly revealed in his photograph of plate 51, fig. 1. Evidently Schlaikjer (1933) did not see Matthew's 1909 statement and figure. He wrote: "I have examined the specimen, and it is very obvious that the slight diastema behind P₂ of which Matthew spoke, presents a small but distinct alveolus. P₂ therefore is two-rooted and was probably as large as P₃." McDowell (1958, p. 175) agreed with Matthew that these alveoli represented P₁ and P₂. Russell (1960, p. 945) believed that Schlaikjer was correct.

Although we have not seen the type specimen, Matthew's 1909 figure seems to be perfectly clear. The alveolus in front is much larger than the one behind it and it seems more likely that a premolar with two roots would have the larger one behind. Furthermore, as seen in the lateral view of Matthew's figure the bone behind the first alveolus is elevated as it is between the other teeth, and the bone is relatively thick between the alveoli. We therefore believe there were four premolars in *M. borealis*.

P₃ and P₄ are somewhat procumbent in the lower half of the crowns in *M. morgani*, but the upper parts curve posteriorly. P₃ is high crowned. Wear on the posterior surface of the protoconid makes it difficult to determine its exact height but it appears to have been as high or nearly as high as the metaconid on P₄. In this young specimen the crown extends at least 3.0 above the edge of the alveolus and about 1.0 below. It is 1.0 wide and nearly oval in outline except at its base. A minute cusp (?paraconid) is present on the anterolingual side of the tooth; this cusp is less prominent than in *M. borealis*. There is less suggestion of a trigonid than in *M. borealis*. The talonid is reduced to a single cusp on the posterolabial corner of the tooth. This cusp is directly labial of the paraconid of P₄, whereas in *M. borealis* the talonid is wider, the cusp is anterior to the paraconid of P₄ and there is a wide, sloping surface on its labial side. P₃ appears to have had a short and slightly bifurcate root, most of which is exposed on the labial side. Unfortunately, after this tooth was illustrated and described the crown was accidentally broken and lost.

P₄ has a well-developed but anteroposteriorly constricted trigonid and a single-cusped talonid. The protoconid is the highest cusp but is only about 0.7 higher than the metaconid. As viewed from the front it curves lingually, and this is more accentuated toward the

apex. When the inner edges of the alveoli of the cheek teeth are held in a horizontal position, it is seen that the tip of the protoconid of P_4 is about equal in height to that cusp on M_1 , and is, therefore, one of the highest cusps in the lower cheek teeth. The height of the protoconid, as measured from the edge of the alveolus on the labial side, is 3.6. Its labial surface is markedly convex anteroposteriorly, but the lingual surface is much less so. The metaconid, on the other hand, is shorter than that cusp on M_1 and M_2 , but appears to be slightly higher than the metaconid on M_3 . The paraconid is about the same height as the hypoconid, whereas in *M. borealis* the paraconid is much higher. The paraconid is a rounded cusp and is well separated from the protoconid by a distinct metaflexid. It also projects forward and in lateral view has a markedly curved anterior edge. The prominent anterior cingulum descending from the paraconid to the anterolabial base of the protoconid in *M. borealis* is nubbinlike in *M. morgani*. The cusp of the talonid is on the posterolabial corner of the tooth and extends backward so that its tip rests under the paraconid of M_1 . In *M. borealis* the cusp is centrally located, and the talonid is wider. A vertical groove separates this cusp from the posterior slope of the protoconid, and there is no low horizontal shelf between the labial base of the talonid and the trigonid, as in *M. borealis*.

In lateral view the spaces between the bases of P_4 and M_1 and between the molars is less in *M. morgani* than in *M. strophensis* and much less than in *M. borealis*. M_1 is longer than M_2 because the paralophid is more flared anteriorly. The trigonids are wider than the talonids on all of the molars, and they become progressively narrower from M_1 to M_3 . The molars are somewhat procumbent in the lower half of the crowns, and the trigonids are well developed. As with the protoconids on the premolars, the protoconids and metaconids in the upper half of the molar crowns curve backward, more so than in *M. strophensis*, and much more than in *M. borealis*. The protoconids are the highest cusps but the metaconids and paraconids are much higher than those cusps on P_4 . The paralophid descends anterolingually from the protoconid then turns rather abruptly more lingually to the paracone. The juncture of the two parts of the paralophid are more distinct on M_1 than on the other molars. The paralophids stand out as projections from the protoconids and abut against the inner edges of talonids of the teeth in front. There are, therefore, spaces between the bases of the molars and between P_4 and M_1 . As on P_4 there is no prominent anterior cingulum descend-

ing from the paraconid to the anterolabial base of the protoconid in *M. morgani*. This feature is well developed in *M. borealis* but only partly so in *M. strophensis*. There is, however, a remnant of this cingulum on the anterior surface of each molar; on M_2 and M_3 this forms a rounded nubbinlike process on the anterolabial surface. It is a mere vestige on M_1 and is well separated from contact with the talonid of P_4 . The crests of the talonid are triangular on M_1 and M_2 . The hypolophid of M_1 forms a transverse crest, the lingual side of which flares back to rest against the tooth behind, whereas the labial side of the hypolophid does not flare back because it rests against the remnant of the anterior cingulum of the tooth behind. On M_2 , however, the nubbinlike anterior cingulum of M_3 fits into a median notch of the hypolophid; consequently the labial extremity of the lophid also flares back. M_3 is slightly displaced lingually in the John Day specimen.

The height of the talonid is equal to more than half the height of the trigonid in *M. morgani* and only less so in *M. strophensis*, whereas in *M. borealis* it is about half, especially on M_1 and M_2 . The anterior spur of the hypoconid connects high on the posterior surface of the protolophid at the midline of the tooth on all three molars. The middle of the hypolophid is only slightly lower than it is at each end; consequently the hypoconulid at the inner end of the crest is nearly as high as the hypoconid and not as distinct as in *M. strophensis*. The entoconid does not stand out as a distinct cusp on the hypolophid. A low crest on M_1 and M_2 extends from the hypoconid diagonally down to the middle of the base of the protolophid. This helps define the wide, sloping, talonid basin that opens lingually. Labially there is a rather wide, nearly vertical, groove between the basal half of the protoconid and the hypoconid. In *M. morgani* and *M. strophensis* there is no labial shelf connecting the base of the hypoconid to the base of the protoconid as in *M. borealis*. The labial surfaces of the hypoconids on all of the molars curve lingually. This is more clearly shown on M_3 than on the other molars, evidently because it is not as worn. The hypoconids are about half as high as the metaconids. The posterior surface of each molar is vertical. As viewed from above, the outline of the molar series is crescentic with the convexity on the labial side. M_2 is approximately equal to M_1 in size. M_3 is much smaller. The talonid of M_3 is relatively wider than in *M. strophensis* and there was probably no entoconid, although the lingual part of the hypolophid is destroyed.

SPECIFIC RELATIONSHIPS AND EVOLUTIONARY TRENDS

Our observations indicate that *M. borealis* Matthew and *M. strophensis* (White), as classified by Russell (1960), are referable to one genus. We feel, however, that *M. borealis* and *M. strophensis*, as well as *M. morgani*, are specifically distinct.

M. morgani is the most advanced species of the genus. Most of its measurements exceed those of the Oligocene species. Its teeth have higher crowns, show a fusion of roots in the premolars, and have undergone a reduction in number. The skull is the widest and deepest of the three genera.

Of the Oligocene species, *M. strophensis* is the more closely related to *M. morgani*. This is evidenced not only by its incipient development of the skull proportions of *M. morgani*, but also in the details of its dental characters. These include the increased molariformity of P⁴ and the modification of cusps and crests into more effective sectorial blades. In not all characters, however, does *M. strophensis* more closely approach *M. morgani* than *M. borealis*. Some features in the teeth of *M. borealis*, such as the discontinuation of the proto-loph connection to the parastyle on the upper molars, are seen in *M. morgani* but not in *M. strophensis*. Several primitive characters are exclusively shared by *M. borealis* and *M. strophensis*. Among others, these include the presence of a "mesostyle" on M¹, and the separation of the small crest at the posterior edge of the hypoconal shelf from the hypocone; these characters are altered or lost in *M. morgani*.

On the basis of this knowledge, *M. strophensis* could be ancestral to *M. morgani*. If this is true, the progressive molariformity of P⁴, the alteration in rostrum proportions to one relatively shorter and wider, the modification of cusps and crests into blades, and the deepening of the rostrum in prelude to higher crowned teeth, are evolutionary trends initiated by *M. strophensis*. If *M. morgani* and *M. strophensis* descended from an earlier common ancestor with *M. borealis*, which seems likely, the evolutionary trend toward *M. morgani* shows a reduction in the kind of submolariformity of P₃ inherited by *M. borealis*. This tooth, and possibly P₁ in the *M. morgani* lineage, became somewhat more caniniform with reduction of the parolophid and the talonid.

COMPARISON OF *Clinopternodus*

The second genus classified in the Micropternodidae is *Clinopternodus*. The only known specimen, *C. gracilis* (Clark), 1936, (in

Scott and Jepson, "The mammalian fauna of the White River Oligocene—Part I"; also Clark, 1937), is part of a left mandible with the canine, P_1 , P_3 , P_4 and M_1 found in an upper member of the Chadron formation.

Clark (1937) states that it is about a third larger than *M. borealis* although it is not much younger than Matthew's species. The size difference between *C. gracilis* and *M. morgani* is much less, but the Oregon species is much younger. This and other features indicate that *Clinopternodus* is more advanced than the contemporary species of *Micropternodus* and evidently represents another lineage in the family.

The lower canine appears to have been slightly larger than in *M. borealis*. The tooth is not known in the other species of *Micropternodus*. The crown of P_1 , although broken off, evidently had one root as in *M. borealis*, but is more rounded and more linguad in position than in the Pipestone Springs species. A foreshortening in the mandible possibly resulted in the loss of P_2 in *Clinopternodus*, although Clark says the specimen is fractured in that area and the evidence for the absence of a tiny alveolus is not conclusive. In *M. borealis* a small alveolus indicates the presence of a reduced P_2 with one root. This area is not known in the mandibles of *M. strophensis* and *M. morgani* but the maxillae in those species indicate that reduction of this interval had taken place. The crowns of P_3 , P_4 and M_1 are more conspicuously procumbent, the upper parts of the crowns more curved lingually, and the tips of the crowns less recumbent than in any species of *Micropternodus*. Insofar as we can see now, these features alone are valid generic distinctions. P_3 is relatively lower crowned than in *M. borealis* and still lower than in *M. morgani*. There is a small anteromedian basal cusp which in *M. borealis* is linguad in position; in *M. morgani* the cusp assumes the same position as in *M. borealis* but is vestigial. There is one cusp on the talonid. P_3 and P_4 are not unlike those teeth in *M. morgani* except for their height, direction and orientation. The talonid equals nearly two-thirds the height of the trigonid, and is consequently more highly elevated with respect to the trigonid than in *M. morgani*.

ANCESTRAL RELATIONSHIPS

The phylogenetic relationships of the early and middle Tertiary families and subfamilies of the insectivores are difficult if not impossible to determine with reasonable accuracy. This is largely due

to the paucity of adequate materials. Well preserved skulls are seldom found and usually upper and lower teeth are not found in association as parts of an individual. Parts of jaws or isolated teeth are sometimes all that we may know of an important genus or subfamily. The interpretation frequently placed on dental features is difficult or impossible to verify because the samples for the most part are insufficient for an insight into variation. Furthermore, different parts of the dentitions are often not available for evaluations of combinations of characters.

Authors differ in their opinions as to which characters represent convergent or possibly parallel evolution and which are indicative of basic relationships. Some feel that cranial morphology, especially the distribution of nerves and blood vessels, location, shapes, and relationships of the orbital bones, construction of the auditory region, etc.—, is the solution to relationships of the higher categories. There can be no doubt about the importance of these studies, but it must be realized there are too few good crania to substantiate the consistency of these characters. The crania and all of their parts also have been subject to evolution, and the trends are as yet even more obscure than those of the dentition. Characters in M_{1-2}^1 are usually fairly reliable in familial classification. Those of M_3^2 are somewhat less so. Fortunately one or more of these teeth can be compared in most specimens. In any event the patterns of the molars must not be ignored irrespective of the other evidence available. The other teeth may be useful, especially P^4 , in the recognition of some families and subfamilies, but the other premolars are usually more subject to adaptive modifications or possess too little complexity. Characters, however, that are stable in one group may not necessarily be so in another.

The most reliable means of determining the phylogenetic relationships of a family is to trace it back through its genera and species to a common origin with another family. No one has been able to do this in the Insectivora, although approximate relationships have been suggested on gross morphology, or on certain combinations of characters, with some confidence.

As might be assumed, we have not been able to determine the ancestry of the Micropternodidae, nor is there conclusive evidence that these genera belong in the Erinaceoidea. Russell's (1960) suggestion, however, that they arose from an erinaceoid ancestry in the Eocene is logical. No known Eocene genus, however, possesses the minimum of the characters one might expect of the ancestral

group. The Leptictidae are generally eliminated on the molariformity of P^4_4 .

Talpavus nitidus Marsh, 1872, as represented by M^1 and M^2 in *Nyctitherium nitidum* Matthew, 1909, pl. 50, 6, A.M.N.H. 11489, has an expanded talon and an emargination of the posterobasal outline at the labial end of the talon much like that in *Micropternodus*. Nevertheless, the presence of a prominent anterolingual cingulum and a deep narrow ectoflexus of the labial margin seem to exclude Matthew's Bridger specimen from the ancestry of *Micropternodus*. Unfortunately P^1 is not known.

The lower molars of *Talpavus*, as seen in Matthew's illustrations (1909, pl. 50, 7) of M_2 and M_3 , are not unlike teeth that might be expected of an ancestral form in the middle Eocene. The talonid, although not high, is higher in relation to the height of the trigonid than in *Micropternodus*, and the anterior spur of the hypoconid that connects to the base of the protoconid at the midline of the tooth is not as high at that point as in the *Micropternodidae*. These *Talpavus* teeth also differ in that the upper half of the trigonids do not curve posteriorly, although this might be attributed to the lack of trigonid height attained by *Micropternodus*. The trigonid bears a prominent anterior cingulum, as should be present in a *Micropternodus* ancestor, and the positions of the paralophids and paraconids, and the talonids being narrower than the trigonids, are early erinaceoid features that are in keeping with the pattern in *Micropternodus*. Apparently a P_4 from Myton Pocket, mentioned by McKenna, Robinson and Taylor (1962, p. 26), is somewhat like *Micropternodus* in the trigonid, but those authors do not mention the talonid. In contrast to *Micropternodus*, McKenna, Robinson and Taylor (1962) state that the entoconid on the molars of A.M.N.H. 55686 from the Bridgerian of Tabernacle Butte is the highest cusp on the talonid. These comparisons seem to indicate that *Talpavus* is not ancestral to *Micropternodus* although some characters are alike in the two genera.

Another middle Eocene genus that may be related is *Scenopagus* (McKenna and Simpson, 1959). M^1 and M^2 also show the possibility of evolving a deep emargination of the posterior basal outline and a wide talon. Like *Talpavus*, however, each of these teeth has an anterolingual basal cingulum, which is not a formidable obstacle because it could gradually be lost. The labial margin has a shallow ectoflexus, as might be expected in the ancestral genus, but the paracone and metacone are much more widely separated than in

Micropternodus, especially on M^1 , and there is a well-developed labial cingulum. The merging of the paracone and metacone could well be an evolutionary trend in some lineages, if a *Scenopagus*-like form gave rise to *Micropternodus*, instead of the twinning of one cusp and eventual wider separation, as has been so widely adopted. Upper premolars like those of *Scenopagus* could give rise to those of *Micropternodus*.

The three lower molars called *Diacodon edenensis* by McGrew (1959, p. 148), and referred to the same genus and species as *Scenopagus mcgrewi* McKenna and Simpson (1959), with the name now recognized as *Scenopagus edenensis* (McGrew), are even less like those of *Micropternodus* than are the lower molars of *Talpavus*.

The mandible described by Matthew (1909) as *Myolestes dasyplex* and the referred specimen of McKenna (1960) offer another possibility. The trigonids of the molars and of P_4 are high and appear to have a slight backward curvature in the upper parts of the crowns, but the talonids are very low. In contrast with *Micropternodus*, the entoconid, not the hypoconid, is the one cusp on the talonid as in *Geolabis*. The upper cheek teeth of *Myolestes* are not known.

TABLE OF MEASUREMENTS

CRANIUM

	<i>M. borealis</i> CM 8674	<i>M. strophensis</i> USNM 18870	<i>M. morgani</i> UCMP 60801
Length:			
as preserved	17.8	16.8	18.3
tip of rostrum through M^3	15.0	—	—
I^2 through M^3 (inclusive)	13.5	—	13.4
I^2 through M^2 (inclusive)	11.5e	—	11.0
canine through M^3 (inclusive)	11.3	11.9	11.8
from posterior border of canine to posterior border of M^2	6.6e	7.0	6.5
P^3 through M^3 (inclusive)	8.8	8.9	9.0
P^3 through P^4 (inclusive)	—	3.6	3.6
M^1 through M^3 (inclusive)	5.8e	5.8	5.8
Width:			
of rostrum at I^2	4.5	—	5.5e
of rostrum at level of I^2	4.6	—	5.1

	<i>M. borealis</i>	<i>M. strophensis</i>	<i>M. morgani</i>
	CM 8674	USNM 18870	UCMP 60801
of rostrum at level of canine	5.7	6.0	7.7
of rostrum immediately behind canine	5.3	5.9	7.7
of rostrum at level of M ² (excluding zygoma)	9.6e	10.8	11.8e
between inner margins of I ³	3.1	—	3.7
between inner margins of canine alveoli	3.0	3.2es	3.4
between inner margin of M ¹ and palate midline	1.4	1.9	2.1
Depth: (excluding teeth; perpendicular to labial edge of maxillary unless otherwise specified)			
of rostrum at level of canine alveolus	2.3	2.4	2.7
of rostrum* immediately behind canine	2.7	2.9	3.7
of rostrum at level of P ³	3.7	3.7	3.7
of rostrum* at alveolus of P ⁴	3.8	3.8	4.8
of rostrum at level of M ¹	5.2	6.0	6.0

UPPER TEETH

	<i>M. borealis</i>	<i>M. strophensis</i>	<i>M. morgani</i>
	CM 8674	USNM 18870	UCMP 60801
Anteroposterior diameter:			
I ¹ (alveolus)	1.0	—	—
I ²	0.7e	—	0.7
I ³	0.5e	—	0.8
C (at alveolus level)	—	1.5	1.7
C alveolus	1.9	1.8	2.4
P ² (alveolus)	0.2	0.2	—
P ³	—	1.4	1.4
P ⁴	2.1	2.3	2.4
M ¹	2.3	2.4	2.4
M ²	1.9	2.0	2.1
M ³	—	1.4	1.9
Transverse diameter:			
I ¹ (alveolus)	1.4	—	—
I ²	0.6e	—	0.7

	<i>M. borealis</i>	<i>M. strophensis</i>	<i>M. morgani</i>
	CM	USNM	UCMP
	8674	18870	60801
I ³	0.5e	---	0.9
C	---	0.9	1.2
C (alveolus)	0.9	1.1	1.7
P ² (alveolus)	0.2	0.2	---
P ³	---	1.3	1.7
P ⁴	2.6	2.4	2.9
M ¹	3.1	2.8	3.1
M ²	2.9	2.8	2.4i
M ³	---	2.2	2.4

MANDIBLE AND LOWER TEETH

Length, P ₃ through M ₃	---	9.1
Depth of mandible, level of M ₂		
Width of mandible, level of M ₂	1.5	2.2
Anteroposterior diameter:		
P ₃	---	1.3
P ₄	---	1.9
M ₁	---	2.4
M ₂	2.2	2.4
M ₃	1.9	2.1
Transverse diameter:		
P ₃	---	1.1
P ₄	---	2.0
M ₁	---	2.0
M ₂	1.9	2.1
M ₃	1.6	1.7
Crown height above alveolus (labial side)		
P ₃	---	2.0
P ₄	---	3.7
M ₁	---	3.8
M ₂	3.1	3.6
M ₃	2.2	3.0e

* depth measured perpendicular to dorsum of cranium

e estimated

es estimated by doubling half-dimension

i incomplete

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